

Taxonomic patterns in the egg to body size allometry of butterflies and skippers (Papilionoidea & Hesperioidea)

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Summary. Former studies have shown that there is an interspecific allometric relationship between egg size and adult body size in butterflies and skippers. This is here re-assessed at the family and subfamily levels in order to determine to what extent the overall trend is uniform through different taxonomic lineages. The results suggest that different subtaxa are characterised by different allometric slopes. Although statistical analysis across species means is known to be potentially misleading to assess evolutionary relations, it is shown that the comparison of apparent patterns (based on species means) with inferred evolutionary trends (based on independent contrasts) may help to understand the evolution of egg size in butterflies. Further, intuitive reconsideration of statistically non-significant results may prove informative. As an example, argumentation in favour of a positive association between large egg size and the use of monocotyledon plants as larval food is presented. Taxa where atypical allometric trends are found include the Riodininae and Theclini (Lycaenidae), the Graphiini (Papilionidae), and the Heliconiinae (Nymphalidae).

Key words. Allometry, butterflies, Hesperioidea, egg size, body size, life-history, Papilionoidea, wing-length

Introduction

Egg size has a relevant position in life-history theory because of its potential links with most other life history traits (Fox & Czesak 2000). In butterflies, these links are believed to include female fecundity, host plant structure, the time required by the larvae to reach their final size, as well as the endurance ability of the egg itself, or of the first instar larvae (Reavey 1992; García-Barros 2000a). Comparative research on the interspecific relations between the egg and adult body sizes among the Papilionoidea and Hesperioidea has demonstrated a robust positive relationship between these two traits (García-Barros & Munguira 1997; García-Barros 2000a). The trend represents a negative allometry, i.e. the eggs of species with largest adults tend to be larger than those laid by small butterflies, but they become proportionally smaller as adult size increases. In other words, the slope (b) of the equation $\log EGG\ SIZE = a + b(\log ADULT\ SIZE)$ is lower than 1.00 (in fact, within the range of 0.4–0.5 when both values are estimated in millimetres). However, it is not known to what extent this general trend applies to every single subordinated butterfly taxon. Alternatively, the trend might be arising from a combination of several distinct patterns characteristic to different phyletic lineages (e.g., Garland & Janis, 1992). This study seeks, first, to check whether the egg to body size allometry holds within the main subtaxa of the papilionoid + hesperioid clade, in order to identify possible exceptions. And second, to determine if particularly small or large eggs (relative to the adult insect size) are restricted to particular taxa, as well as to discuss some possible reasons of the patterns discovered.

The size of each of the species within a clade was inherited – at least in part – from a shared ancestor. Hence, mean sizes of individual species are not statistically inde-

pendent, one necessary pre-requisite of standard regression procedures (for butterflies: García-Barros 2000c). The method of independent contrasts is one of the comparative procedures proposed to solve this problem (Felsenstein 1985; Starck 1998), and will be used in this study. However, the raw species means are not devoid of interest, for two reasons: First, because they can be used to describe present patterns which, when statistically significant, have a predictive value (paradoxically, one reason why this may work is phylogenetic inertia, the same reason why evolutionary relations cannot be directly inferred from the data). And second, that comparisons of the two approaches are by themselves informative whenever it is kept in mind that observable patterns among raw species data do not necessarily represent evolutionary trends, and that the opposite is true for regressions done on independent contrasts.

Methods

The information used in this work is the same as described in García-Barros (2000a, b, c). No attempt has been done to update either the size estimates nor the phylogenetic hypotheses underlying the comparative analysis, even if new evidence of both kinds has become available more recently (e.g. Penz 1999; Brower 2000; Kitching *et al.* 2000; Martin *et al.* 2000; Harvey & Hall 2002). This facilitates a direct comparison with the results presented elsewhere (García-Barros 2000a). The author assumes that, as further work on butterfly life-histories and phylogenetic reconstruction progresses, the results dealt with here might be substantially modified.

The data consisted of two linear estimates from each out of 1183 species: egg size (egg volume^{1/3} in mm), and adult size (the length of adult fore-wing in mm). Both were transformed to decimal logarithms before any statistical treatment. Full details can be found in García-Barros (2000b). Two parallel sets of analyses were carried out, using two versions of the same data: the species data points (the log-transformed egg and adult size estimates), and the taxonomically independent contrasts calculated for those two traits. The independent contrasts are weighted differences between the values of a variable in the taxa derived from the same node in the cladogram or taxonomic arrangement (Harvey & Pagel 1991; Garland *et al.* 1992; Starck 1998). These were obtained using the program CAIC (Purvis & Rambaut 1995), as specified in García-Barros (2000a). The contrasts can be analysed in the same way as the original data, except that regressions have to be forced through the origin. This means that there is no intercept, and hence the allometric equation becomes $EGG\ SIZE\ contrast = b(ADULT\ SIZE\ contrast)$ (e.g. Garland *et al.* 1992).

The analyses were performed using the computer package STATISTICA (StatSoft 2000), and included: (1) A brief description of the variation of egg size in the main taxonomic groups (family, subfamily), and their associated adult sizes. (2) Determining the allometric relations of egg to body sizes by regression. Only taxa at or above the tribe level, where nine or more contrasts could be calculated, were included in this and subsequent steps. Least Squares Regression (LSR) was used throughout the study, but Reduced Major Axis (RMA) slopes were calculated for comparison. In brief, these two regression models differ in the way used to minimize the distances between the

data points and the regression line. LSR uses the shortest distance measured from the axis that represents the independent variable, while RMA regression minimizes the distances relative to both (X, Y) axes (details and further references can be found in Harvey and Pagel, 1991, and in the discussion). (3) Comparing the slopes of the regression lines fitted to the families and subfamilies, by means of pairwise analyses of the covariance (ANCOVA) of egg size by taxonomic levels with adult size as the covariate. The effect of two factors crossed (family or subfamily, and adult size) was tested (e.g. Garland *et al.* 1992). Taxa where egg and body size were not correlated were discarded for this purpose. (4) Finally, the mean relative egg sizes were compared to the common trend, in order to identify families or subfamilies where unexpectedly high or low relative egg size values were found. The effect of one categorical variable containing codes for the families and subfamilies was tested by ANCOVA, with adult size as the covariate. The residuals of the regressions of egg size on adult wing size were used for graphic purposes.

Results

The frequency distributions of the egg and adult sizes of each of the five families are shown in Figure 1. Mean adult wing length increased following the order: Lycaenidae, Hesperidae, Pieridae, Nymphalidae, and Papilionidae. Mean egg size increased accordingly from Lycaenidae to Papilionidae, with the exception that Hesperidae and Pieridae appeared in reverse order. The taxonomic arrangement could significantly explain the variance of the original egg size data (controlling for adult size) both at the family level (ANCOVA: $F_{4, 1088} = 84.73$, $P < 0.0001$), and at the subfamily level (ANCOVA: $F_{14, 1078} = 62.71$, $P < 0.0001$), and so a degree of 'taxonomic conservatism' in relative egg size is evident in the original data.

Not surprisingly, the smallest (in absolute terms) eggs are those laid by the tiniest lycaenids, in particular some representatives of the tribe Polyommataini (Lycaeninae) such as *Brephidium*, *Zizina* or *Hemiargus* (e.g. Dethier 1940; Clark & Dickson 1971) with estimated egg volumes of 0.015 to 0.03 mm³. Conversely, the largest eggs are those of the troidine papilionids (up to 20 mm³ or more). The egg of *Ornithoptera tithonus* de Haan measures 4.1 mm in diameter (Parsons 1995), and its volume is 1,700 times larger than that of the smallest lycaenid eggs. Other representative examples of large butterflies laying large eggs include the nymphalid subfamilies Charaxinae or Morphinae (e.g. Hoffmann 1938; Casagrande & Mielke 1985; Igarashi & Fukuda 1997; Urich & Emmel 1991). Species that lay unexpectedly large eggs relative to their wing size include some members of the nymphalid genera *Dophla*, *Dynastor* and *Agrias*, as well as several Hesperidae-Trapezitinae (e.g. Atkins 1978). Opposite to these, some Pieridae (*Phoebis*, *Tatochila*, *Antheos*) and Nymphalidae (*Hypolimnas*, *Pandoriana*) lay remarkably smaller eggs than expected (van Son 1979; Shapiro 1987; García-Barros 2000d).

The regression statistics are given in Table 1. Regressions based on contrasts were generally more conservative. Irrespective of the kind of data used, no correlation was found for the Graphiini (Papilionidae), the Theclini (Lycaenidae), the Heliconiinae

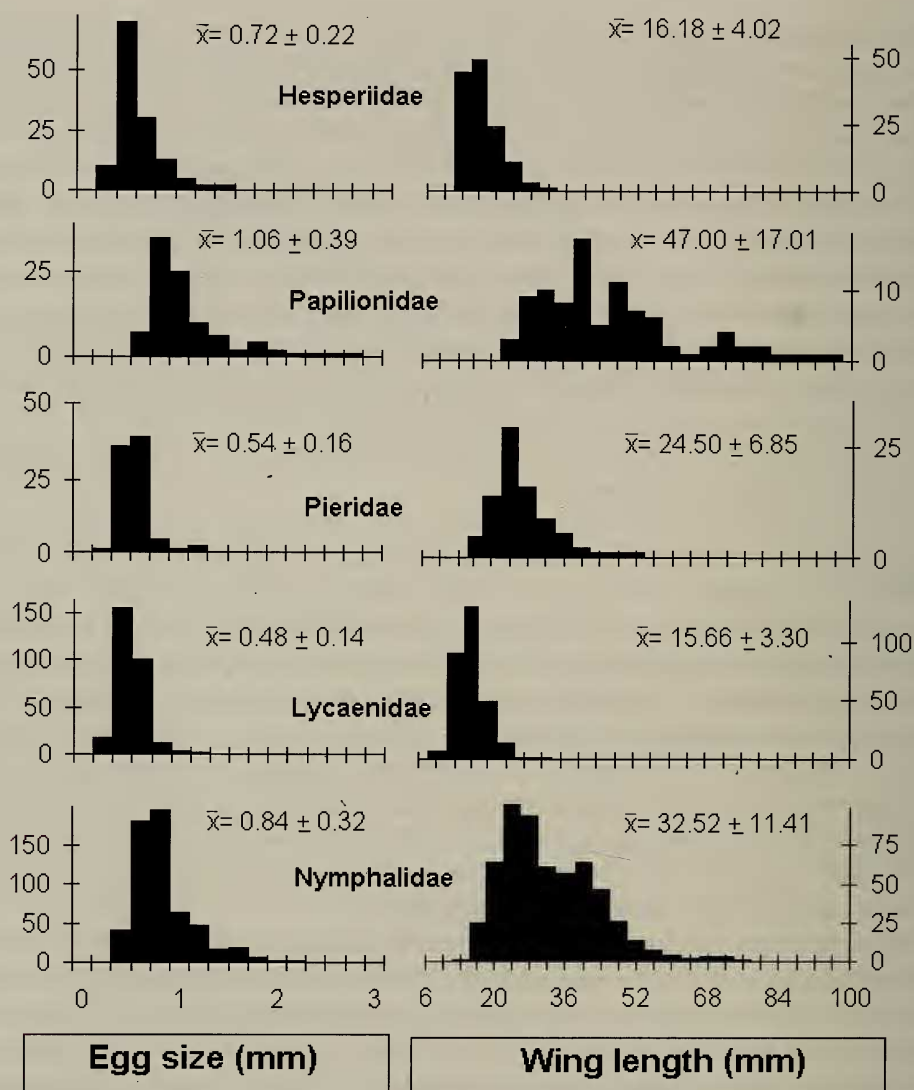


Fig. 1. Frequency distributions of egg size (left column) and wing length (right column) of the species included in the data set, arranged by families. Note that the Y axis scales differ among the histograms. The arithmetic average \pm 1 standard deviation are included in each histogram.

(Nymphalidae), nor the two heliconiine tribes Acraeini and Heliconiini. Some correlations that were supported by the analysis of species means vanished when the contrasts were used: HesperIIDae-Trapezitinae, Lycaenidae-Eumaeini, and the family Lycaenidae as a whole. Other relationships (e.g. in Papilionini swallowtails and within the Danainae nymphalids) appeared to be more robust when based on contrasts than when estimated from the original data. The Riodininae (Lycaenidae) were remarkable for representing the single taxon to display a significant, negative correlation across contrasts, but none with raw species data. A few representative plot graphs are presented in the Figs 2–3.

Table 1. The allometric relationship between egg size and adult body size in butterfly families, subfamilies and tribes, derived from species data and independent contrasts. Only taxa where nine or more contrasts could be calculated are included. N = number of species or contrasts, r = Pearson's coefficient of correlation (**** – $P < 0.0001$, *** – $P < 0.001$, ** – $P < 0.01$, * – $P < 0.05$, ns – not significant, $P > 0.05$). Least squares regression (LSR) and reduced major axis (RMA) slopes are given in all instances, but note these are not relevant when the correlation is not significant. Regressions of contrasts were forced through the origin, and thus the intercept is equal to 0.00.

TAXON	Species data						Independent contrasts				
	N	r	P	a	$b(\text{LSR})$	$b(\text{RMA})$	N	r	P	$b(\text{LSR})$	$b(\text{RMA})$
Butterflies	1183	0.71	****	-1.04	0.62	0.87	461	0.41	****	0.49	1.22
HESPERIIDAE	132	0.50	****	-0.91	0.63	1.25	50	0.55	****	0.55	1.00
Hesperiinae	63	0.78	****	-1.41	1.06	1.36	30	0.59	***	0.74	1.23
Trapezitinae	28	0.40	*	-0.77	0.58	1.43	9	0.54	ns	0.49	0.92
Pyrginae	38	0.46	**	-0.64	0.35	0.76	11	0.59	*	0.21	0.36
PAPILIONIDAE	94	0.76	****	-1.21	0.73	0.96	47	0.73	****	0.71	0.97
Pamassiinae	34	0.50	**	-0.97	0.59	1.19	11	0.72	**	0.43	0.59
Papilioninae	60	0.81	****	-1.66	0.99	1.21	34	0.73	****	0.78	1.06
Graphiini	14	0.16	ns	-0.46	0.24	1.44	9	0.61	ns	0.63	1.04
Troidini	22	0.89	****	-1.74	1.05	1.18	11	0.84	***	1.20	1.43
Papilionini	24	0.44	*	-0.81	0.48	1.09	13	0.74	**	0.49	0.67
PIERIDAE	84	0.51	****	-1.04	0.54	1.05	31	0.38	*	0.32	0.85
Pierinae	59	0.57	****	-1.14	0.61	1.07	15	0.34	**	0.31	0.92
LYCAENIDAE	298	0.50	****	-1.13	0.67	1.34	113	0.15	ns	0.13	0.85
Riodininae	32	0.04	ns	-0.40	0.05	1.12	15	-0.51	*	-0.27	0.54
Lycaeninae	248	0.54	****	-1.21	0.73	1.35	85	0.35	*	0.30	0.86
Theclini	43	0.28	ns	-0.56	0.24	0.87	14	0.07	ns	0.09	1.18
Eumacini	37	0.53	***	-0.99	0.61	1.15	19	0.21	ns	0.22	1.06
Polyommattini	122	0.42	***	-0.89	0.39	0.93	45	0.31	*	0.26	0.84
NYMPHALIDAE	575	0.63	****	-1.07	0.65	1.03	276	0.41	****	0.59	1.45
Nymphalinae	58	0.61	****	-0.95	0.47	0.77	20	0.70	**	0.64	0.92
Heliconiinae	105	0.22	ns	-0.72	0.34	1.57	55	0.16	ns	0.36	2.26
Acraeini	18	0.37	ns	-0.71	0.31	0.83	15	0.34	ns	0.24	0.72
Heliconiini	86	0.16	ns	-0.64	0.29	0.85	39	0.18	ns	0.54	2.92
Ithomiinae	65	0.49	****	-0.88	0.48	0.98	41	0.32	*	0.36	1.11
Danainae	27	0.51	**	-1.09	0.64	1.25	20	0.70	***	0.99	1.43
Limenitinae	40	0.67	****	-1.67	1.04	1.55	18	0.57	*	0.62	1.09
Charaxinae	62	0.70	****	-1.46	0.96	1.39	25	0.58	**	0.79	1.34
Satyrinae	175	0.44	****	-0.88	0.56	1.25	72	0.40	***	0.64	1.58
Elymniini	35	0.36	*	-0.94	0.62	1.73	10	0.43	ns	1.22	2.85
Satyrini	138	0.39	****	-0.72	0.44	1.12	58	0.46	***	0.41	0.91

Whenever a significant correlation was found, the LSR slopes had positive values between +0.21 and +1.20 (except for the Riodininae, Table 1), and RMA slopes were often close to or above 1.00. The tests for heterogeneity of the slopes are summarised in Tables 2 and 3. Family and subfamily mean relative egg sizes, as well as mean relative egg size increases, are compared with the overall relation depicted in Figure 4. The differences between pairs of taxa are presented in Tables 4 and 5.

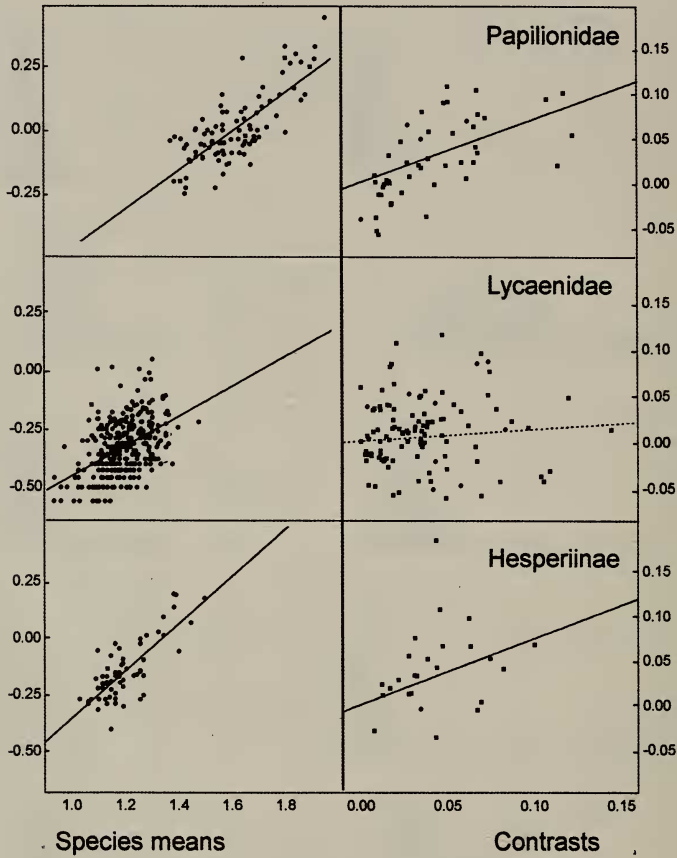


Fig. 2. Sample plots to illustrate the relationship between egg size (Y axis) and adult size (X axis) at different taxonomic levels: families Papilionidae and Lycaenidae, and subfamily Hesperinae (Hesperiidae). Left column, as estimated from the logarithmically transformed species data. Right column, based on independent contrasts. The trend lines illustrated are those fitted by least squares regression. A dotted line indicates non-significant correlation. Note that the scales of the left and right columns are not the same. See Table 1 for further details.

Table 2. Paired comparisons to test the significance of differences between the slopes of the regressions of egg size on adult size of the five butterfly families. The values are the *F* statistic for the interaction between the factors 'family' and 'adult size' in an analysis of the variance of egg size by families using adult size as a covariate (1 d.f.). * - $P < 0.05$, nt - not tested (the differences between the Lycaenidae and other families, based on contrasts, were not tested since no correlation was found within the lycaenids). The comparisons based on the independent contrasts are given above the diagonal, and those based on species data points below the diagonal. Only two pairs of families were found to have significantly different slopes, based on independent contrasts. None of the differences based on species data were significant ($P > 0.24$ in all instances).

	Hesperiidae	Papilionidae	Pieridae	Lycaenidae	Nymphalidae
Hesperiidae	-	3.98*	0.00	nt	0.02
Papilionidae	0.83	-	4.83*	nt	2.79
Pieridae	0.06	1.35	-	nt	0.05
Lycaenidae	0.00	0.89	0.10	-	nt
Nymphalidae	0.01	1.19	0.12	0.00	-

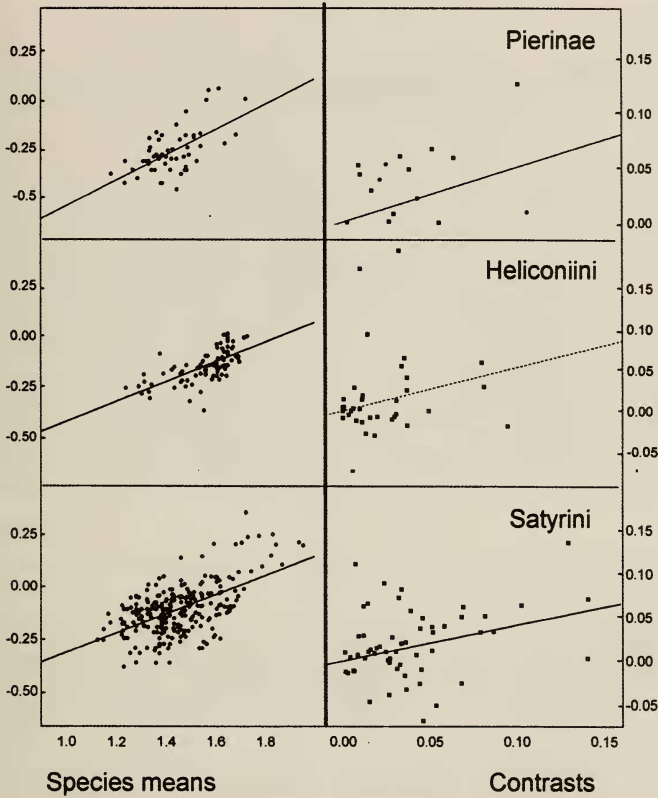


Fig. 3. Plots showing the relationship between egg size and adult size in the subfamily Pierinae (Pieridae), and the tribes Heliconiini (subfamily Heliconiinae, Nymphalidae) and Satyrini (subfamily Satyrinae, Nymphalidae). Details as in Figure 2.

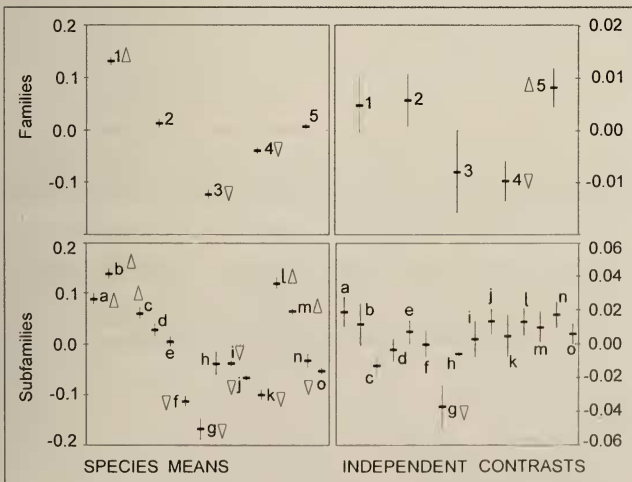


Fig. 4. Plots illustrating relative egg size (based on species means) and relative egg size increase (based on independent contrasts) in butterfly families, and selected subfamilies. The values were calculated as distances from the common trend (residuals from the regression), based either on species data points or on independent contrasts. The vertical bars indicate ± 1 standard error. The common trend is represented by the dotted line, and values above or below 0.00 indicate either proportionally large or small egg size. The taxa referred to are 1 = Hesperiiidae, 2 = Papilionidae, 3 = Pieridae, 4 = Lycaenidae, 5 = Nymphalidae, a = Hesperiiinae, b = Trapezitinae, c = Pyrginae, d = Parnassiinae, e =

Papilioninae, f = Pierinae, g = Riodininae, h = Lycaeninae, i = Heliconiinae, j = Nymphalinae, k = Limenitinae, l = Charaxinae, m = Satyrinae, n = Danaeinae, and o = Ithomiinae. Taxa marked with a triangle have a mean that departs significantly from the common trend ($P < 0.05$ or below).

Table 3. Paired tests for the significance of the differences between the slopes of the subfamilies in Table 1. *F* values, 1 *d.f.*, details as for Table 2 (* – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$). The upper right half of the matrix summarises the comparisons of slopes derived from independent contrasts, and the lower left half those between slopes derived from species data. No comparison was attempted for those subfamilies that did not show a significant relationship between egg size and adult size (nt – not tested).

Taxon	Hesp.	Trap.	Pyr.	Par.	Pap.	Pier.	Rio.	Lyc.	Nym.	Lim.	Char.	Sat.	Dan.	Itho.
Hesperiinae	----	nt	0.51	0.01	1.46	0.04	6.81*	0.69	0.18	0.12	0.01	0.07	0.18	2.68
Trapezitinae	3.06*	----	nt	nt	nt	nt	nt	nt	nt	nt	nt	nt	nt	nt
Pyrginae	18.79***	0.81	–	1.34	4.06*	0.38	4.08	0.06	0.25	0.86	0.42	0.15	1.68	0.31
Parnassinae	4.52*	0.00	1.35	–	2.13	0.01	11.77**	0.44	0.13	0.20	0.00	0.00	0.40	2.55
Papilioninae	0.05	2.72	18.65***	4.09*	–	2.88	28.29***	9.69**	4.46*	0.41	1.42	1.45	0.41	14.81***
Pierinae	5.32*	0.11	3.61	0.14	5.02*	–	7.74**	0.45	0.06	0.33	0.01	0.01	0.47	2.61
Riodininae	nt	nt	nt	nt	nt	nt	–	7.75**	8.05**	7.45*	5.72*	3.58	11.68**	1.90
Lycaeninae	4.86*	0.19	4.20*	0.25	4.92*	0.06	nt	–	0.13	1.77	0.39	0.69	1.85	1.84
Nymphalinae	19.55***	0.44	0.13	0.77	20.19***	3.17	nt	4.98*	–	0.63	0.10	0.07	0.94	2.02
Limnitiinae	0.00	1.56	9.26**	2.30	0.01	3.23	nt	3.06	10.30**	–	0.16	0.13	0.01	4.05*
Charaxinae	0.27	1.96	11.78**	2.54	0.13	2.50	nt	2.03*	11.58**	0.12	–	0.00	0.24	1.96
Satyrinae	22.39***	0.07	1.21	0.25	24.82***	2.33	nt	5.84*	0.72	13.36***	12.00**	–	0.14	1.81
Danaeinae	2.98	0.04	1.46	0.02*	2.62	0.04	nt	0.09	0.85	1.47	1.62	0.37	–	4.71*
Ithomiinae	14.25***	0.10	0.64	0.32	14.17***	1.62	nt	2.28	0.22	7.75**	8.36**	0.03	0.45	–

Table 4. Summary of the between-family differences in relative egg size (controlling for adult size) based on a multiple range test. The upper right half of the matrix shows the relative egg size increases based on independent contrasts, and the lower left half refers to results based on the species averages (relative egg size). * – significant at the $P < 0.05$ level or below (the differences themselves are not shown for simplicity), ns – not significant.

	Hesperiidae	Papilionidae	Pieridae	Lycaenidae	Nymphalidae
Hesperiidae	–	ns	ns	ns	ns
Papilionidae	*	–	ns	ns	ns
Pieridae	*	*	–	ns	ns
Lycaenidae	*	ns	*	–	*
Nymphalidae	*	ns	*	*	–

Table 5. Summary of the between-subfamily differences in relative egg size increase (upper right half), and relative egg size (lower left half). Only subfamilies where 9 or more independent contrasts could be calculated were compared. All other details as for Table 4.

Taxon	Hesp.	Trap.	Pyr.	Par.	Pap.	Pier.	Rio.	Lyc.	Hel.	Nym.	Lim.	Char.	Sat.	Dan.	Itho.
Hesperiinae	–	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns
Trapezitinae	*	–	ns	ns	ns	ns	*	ns	ns	nt	nt	ns	ns	ns	ns
Pyrginae	*	*	–	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Parnassinae	*	*	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Papilioninae	*	*	*	*	–	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
Pierinae	*	*	*	*	*	–	ns	ns	ns	ns	ns	ns	ns	ns	ns
Riodininae	*	*	*	*	*	*	–	ns	*	*	*	*	*	*	*
Lycaeninae	*	*	*	*	ns	*	*	–	ns	ns	ns	ns	*	ns	ns
Heliconinae	*	*	*	*	*	*	*	ns	–	*	ns	ns	ns	ns	ns
Nymphalinae	*	*	*	*	*	*	*	*	*	–	ns	ns	ns	ns	ns
Limnitiinae	*	*	*	*	*	ns	*	*	*	*	–	ns	ns	ns	ns
Charaxinae	*	*	*	*	*	*	*	*	*	*	*	–	ns	ns	ns
Satyrinae	*	*	ns	*	*	*	*	*	*	*	*	*	–	ns	ns
Danaeinae	*	*	*	*	*	*	*	ns	ns	ns	*	*	*	–	ns
Ithomiinae	*	*	*	*	*	*	*	ns	ns	ns	*	*	*	ns	–

Discussion

Taxonomic heterogeneity. The slopes of the lines fitted to the species means are markedly homogeneous at a high (family) taxonomic level, but differences arise at the sub-family level. The overall slope based on the independent contrasts ($b = 0.49$) appears to mask a number of non-coincident trends. These include taxa without evident allometry (e.g. Lycaenidae-Theclini, Nymphalidae-Heliconiinae), as well as phyletic lineages characterized by slopes that differ significantly from the overall allometry pattern (e.g. Pieridae, Papilionidae, Hesperiiidae). For analogous reasons, the interpretation of significant differences between family-level slopes is not straightforward. For instance, the differences between the skipper and the swallowtail slopes are basically a consequence of those that exist between the subfamilies Papilioninae (Papilionidae) and Pyrginae (Hesperiiidae), respectively. This suggests that detailed quantitative comparisons will require a more narrowly defined taxonomic scenario. It is likely that the general pattern merely represents an average trend, not a real property of a number of the subtaxa analysed.

Regression lines and models. Determining accurately the regression slopes is interesting for further evolutionary argumentation, since negative allometry (slope $b < 1.0$) would lead to predict enhanced fecundity in large bodied butterfly species (García-Barros 2000a). This is exactly the general pattern in butterflies that one would infer from the LSR slopes (range of significant b values: 0.35–1.06 for species data, 0.21–1.27 for independent contrasts). In contrast the usually higher RMA slopes (most b values > 1.0 , irrespective of the type of analysis) would mostly lead to reject the idea of a structural relation between body size and fecundity. LSR tends to underestimate the slope, and this effect is the stronger the lower the correlation coefficients are (details in Rayner 1985; LaBarbera 1989; Harvey & Pagel 1991; Riska 1991; Garland *et al.* 1992). Which method should be preferred depends on the ratio of error variance between the two variables. Although there is some support for applying LSR to the present data set (McArdle 1987; García-Barros & Munguira 1997), estimates of the measurement errors in the variables would facilitate the choice of a regression model. Such estimates could be calculated from independent estimates of the egg and adult sizes of each species.

Wing length and body size. The results of this work assume that wing length is well correlated to overall body size (e.g. body weight: Miller, 1977, 1997), and that the relationship between both is roughly constant. This is probably the case in most instances. However, some degree of architectural heterogeneity may occur even among related species, for instance, resulting from selection for flight ability, mating strategies, or palatability (Betts & Wootton 1988; Chai & Srygley 1990; Marden & Chai 1992; Wickman 1992; Corbet 2000; Hall & Willmott 2000). In order to improve the analyses, one would have to resort to more precise measures of body mass, which however are still unavailable for most of the species.

Conflicting evidence and egg size as related to monocotyledon larval feeding. Conflict between the trends based on the species values and those supported by the independent contrasts may be of interest for evolutionary speculation. For instance, the

Hesperiidae-Pyrginae would be said to lay relatively large eggs based on the original data. However, the regression based on contrasts indicates that evolutionary shifts in the relative egg size of these skippers have most often been below the butterfly average. This suggests a 'large egg-stage' as plesiomorphic in this group, followed by frequent parallel shifts to proportionately lower egg sizes.

Patterns that vanish after controlling for taxonomic effects are likely to reveal single evolutionary novelties acquired by an ancestral taxon, and subsequently inherited by all descendant species. These are identified in the transformed data by one, or a few positive contrasts, so that the evolutionary event will have no statistical significance (Nylin & Wedell 1994). The volume of the eggs of species with grass-feeding larvae provides an example. The Poaceae have leaves with a parallel array of sclerenchyma fibres and contain high levels of silica, which make them difficult to chew (Bernays & Barbehenn 1987). Large egg size should improve the survival of the correspondingly larger newly hatched larvae when these have to feed on tough plant leaves (Wiklund & Karlsson 1984; Braby 1994). The longer distance between the mandible bases would allow for widest bites, and the widest mandibular muscles would permit a net increase in mandibular strength (cf. Nakasuji 1987). However, tests for a positive relationship between egg size and larval monocot feeding have not produced any convincing results (García-Barros 2000a). A more intuitive reconsideration of the hypothesis is presented in Table 6. Two skipper subfamilies (Hesperiinae, Trapezitinae) have larvae that feed on monocotyledonous plants. The members of both groups lay proportionally larger eggs than the Pyrginae, which use dicot hosts. Further, the slope of the egg to body size relation is lower in the Pyrginae. The association between large egg size and larval monocot-feeding should hence be regarded as a possibility in the skippers, although this probably represents a single evolutionary event related to an ancestor of the entire Hesperiinae + Trapezitinae clade. The same might hold for the satyrine nymphalids, and perhaps other butterflies (Table 6).

Are small eggs selected for? Small eggs might have been selected for under a number of circumstances, such as endophytic or cryptic larval habits (Reavey 1993), or increased female fecundity. Everything else being equal, egg size reduction should imply a longer larval development time, and hence a possible trade-off between fecundity and adult size. This could in turn be compensated for by larval feeding being specialised on nutrient-rich parts of the host (Mattson 1980; McNeill & Southwood 1978; Slansky 1993). These circumstances make one recall the family Lycaenidae, for in fact these butterflies lay smaller eggs than expected for their adult body sizes (at least when the average is considered, Fig. 4). Further, egg size and body size are only loosely linked in the Polyommata, and apparently unrelated in the Theclini (Table 1). Since lycaenid life-histories are often complex, a varied array of specializations may contribute to obscure allometric trends in these insects.

Wiklund *et al.* (1987) found no correlation between the egg weights and female body weights of North European pierids, and argued that such pattern could result from selection for increased fecundity through increased body size. The present study shows that egg size and body size are correlated in the Pieridae. However, the slope of the relationship measured on independent contrasts is comparatively low, as it is for

Table 6. Evidence concerning the possible association between larval feeding on monocotyledonous plants and large egg size. The figures given in brackets are the egg sizes expressed as percentages of wing length, obtained from the species values that were hierarchically averaged following the taxonomic arrangement. An asterisk indicates that the estimate is based in only one or two species. The signs (+, –) denote the direction of hypothetical changes in relative egg size (left to right column within each row). Although the direction of the shift within the Morphinae depends on the phylogenetic hypothesis assumed, it would require no less than one change to larger egg size in combination to one shift to monocots. One of the correlated changes has to be deleted if the Brassolinae were shown to be the sister group of the Satyrinae or Morphinae. If the two hypothesised reversals to non-monocotyledon hosts are excluded, a majority of the events of monocot colonisation happen to be associated with increases in relative egg size.

Family	Nearest related taxon with dicot hosts	shift	Taxon feeding on monocots	shift	Possible reversals to non-monocots
Hesperiidae	Pyrginae (3.61) Coeliadinae (2.69)	+	[Hesperiinae plus Trapezitinae (4.86)]	+	<i>Acleros</i> (Hesperiinae) (4.49)
Lycaenidae	Riodinids (2.4) <i>Mesosemia</i> (2.0*)	+	<i>Napaea</i> (2.8*)		
	Other Eumacini (2.6)	+	<i>Eooxylides</i> (4.2*)		
	<i>Jamides bochus</i> (1.8*)	+	<i>J. alecto</i> (2.45*)		
Nymphalidae	Other Limenitinae Euthaliiti (3.6)	–	<i>Bebearia</i> (2.3*)		
	Other Nymphalids (2.3)	+	Satyrinae (2.8) or Brassolinae (2.8)	–	Ragadiini (Satyrinae) (2.5*)
	<i>Morpho?</i> (2.1) or other Morphinae? or other nymphalids? (2.3)	+?	<i>Antirrhoea</i> (3.4*) <i>Amathusiini</i> (2.6)		

the best represented subfamily, Pierinae. Again, the comparison between the apparent relationship and the one derived from the comparative study suggests that proportionally small eggs represent a basal trait within the Pieridae. This is difficult to judge with precision because of the high variance of the contrasts, but it may be stated with some confidence for the subfamily Pierinae at least (see Fig. 3). An interpretation is that the present pierid pattern represents the result of ancestral reduction in relative egg size, probably combined with structural negative allometry. The ultimate reason could well have to do with selection for high fecundity, although again other ecological specializations (such as larval feeding on highly nutritious substrates) cannot be ruled out.

Can the evolution of egg and body size be negatively correlated? According to the data collected, the evolution of egg size in the Riodininae (Lycaenidae) has proceeded following an inverse trend relative to wing size. Negative allometry (slope between 0.0 and 1.0) is commonplace in most animal groups (Reiss 1989), while a negative correlation between increases of egg size and adult body size is surprising. The process implies a generalised minimisation of egg size following evolutionary increases in adult size, and oversized eggs in species selected for small body size. Re-assessing this relationship on the light of new evidence proves necessary. There is of course the possibility that the number and quality of the size estimates from riodinids was inadequate, or that the taxonomic arrangement adopted (basically following DeVries 1997) is particularly unrealistic. A number of recent descriptions of riodinine eggs (Downey

& Allyn 1980; DeVries 1997) prove that an amount of material is being collected and stored in scientific collections. This, together with new life-history data from hitherto poorly known species, should soon facilitate a reassessment of the egg to body size allometry in the metalmarks.

Absence of allometry. The Heliconiinae (sensu Harvey, 1991) show no sign of egg to body size allometry, and the same applies to the heliconiine tribes Acraeini and Heliconiini. To the extent that the data are reliable, it is likely that the diversification of size in these butterflies may have been subject to fast evolution in response to varied environmental variables. The adult biology of *Heliconius* is peculiar in several respects, such as the ability to gather amino acids from pollen and their potentially long adult life (e.g. Dunlap-Pianka et al. 1977; Dunlap-Pianka 1979; Brown 1981). Does pollen-feeding release egg size evolution to operate within broader limits than in other butterflies? In theory, an important contribution of adult-acquired resources to egg production could relax the egg size to egg number trade-off (Fox & Czesak, 2000). This, together with several other circumstances that may have a bearing on size and fecundity (mimicry, migration), render the Heliconiinae another relevant case to determine how selection for certain life-history trait values might affect the combined evolution of egg and adult sizes. Similarly intriguing absences of egg/body size correlations in the hairstreaks (Lycaenidae, Theclini) and the Graphiini (Papilionidae) also deserve further attention.

Conclusions

Within the limits imposed by the data, it is clear that butterfly egg size is overall related to adult body size by negative allometry, and that this is equally valid for most of the clades at the family, subfamily, and tribe levels. There are some relevant exceptions, and these require further research. However, as far as the quantification of the allometric relation is concerned, things are not so clear. The results suggest that the general pattern (above the family level) may result from a combination of heterogeneous allometric relations within the subordinated subtaxa. Determining the slopes with more accuracy is the pertinent next step in this research program. This will prove feasible only to the extent that more, and more accurate data, become available, and as far as the degree of phylogenetic resolution in this Lepidopteran group is substantially increased. Published butterfly life-histories represent a vast amount of data suitable for comparative work, and this has only superficially been explored so far. Desirable data such as egg weight are not easy to gather under field conditions, but reasonable estimates of egg volume can be obtained without much difficulty, e.g. from scale drawings of egg profiles, slides, or similar means. Hopefully, some of the patterns described here will soon be ready for re-consideration.

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